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Marine community effects of two colonial zoanthids in intertidal habitats of the Canary Islands

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ABSTRACT

Rising ocean temperatures as consequence of climate change has led to increased populations of species with tropical affinities, generating a tropicalization process of the biota. In this sense, an increase in populations of the zoanthids *Palythoa canariensis* and *Zoanthus* sp. is expected for the Canary Islands being able to change local habitats and biodiversity. Within this study the potential of these species to modify the composition of their associated fauna in intertidal pools of the Canaries was assessed. The composition and biodiversity of communities in intertidal habitats dominated by *P. canariensis* and *Zoanthus* sp. were compared with habitats dominated by macroalgae. Samples were collected in order to quantify the mesofauna, and coverage of algae and zoanthids colonies were assessed. Results showed significant differences in the composition of the associated fauna between both kind of habitats, as well as an increase in species diversity and richness in habitats dominated by colonies of both zoanthids. The high potential of *P. canariensis* and especially of *Zoanthus* sp. to transform the habitat and associated communities of invertebrates in intertidal environments of the Canary Islands was demonstrated. Given the expected climate change scenario for the future that will benefit the expansion of these key zoanthids, important changes in the biodiversity and potential alterations in natural ecosystems are expected for the Archipelago.

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1. Introduction

A rising number of studies have been carried out trying to understand and predict the effects of climate change on the physiology and distribution of marine organisms (Root et al., 2003; Harley et al., 2006). These physico-chemical changes in the marine environment could have serious deleterious consequences in the diversity of biological communities and for the proper behaviour of marine ecosystems (Ling, 2008; Zarnetske et al., 2012). The increase in ocean temperatures is probably the most evident effect of climate change, because it alters patterns of distribution and phenology of marine organisms modifying the physiological processes that allow them to adapt and survive to different specific ranges of temperature (Harley et al., 2006). An example of these effects is the so-called tropicalization processes, which is the increased occurrence and spread of thermophilic biota (indigenous or introduced species), favoured by the movement of species beyond their normal limits of distribution and the trend to disappearance of native species that are in their limit of thermal tolerance (Bianchi and Morri, 2003; Vergés et al., 2014; Brito et al., 2017). As consequences of these displacements, native populations and even local ecosystems structure and function can be affected (Lodge et al., 1993). In many places, such as at the Northern coast of Spain (Galicia) or the Mediterranean Sea, the lost or replacement of native species due to the appearance of exotic tropical species, has been confirmed (Bianchi and Morri, 2003; Streftaris et al., 2005; Galil, 2007). These species show abilities to dominate new regions, altering local ecosystems with important social and economic implications (Sakai et al. 2001; Vergés et al., 2014; Wernberg et al., 2016).

The Canary Islands, due to their subtropical location, are considered a good reference region to better understand the tropicalization of marine systems (Kaimuddin et al., 2016). In the last decades, the mean Sea Surface Temperature (SST) has increased 1 °C for this region (Aemet, 2008), being especially relevant during winter months (Vélez-Belchí et al., 2015). The main biological consequences of these changes have been the arrival and establishment of numerous non-native species of tropical origin in the Canaries (e.g. Brito et al., 1995, 2011; Otero-Ferrer et al., 2015; Herrera et al., 2017). Some good examples of this phenomenon are the occurrence of colonies of the fire coral *Millepora* sp. from the Caribbean in the Islands (Clemente et al., 2011; López et al., 2015), the amphipods *Caprella scaura* Templeton, 1836 from the

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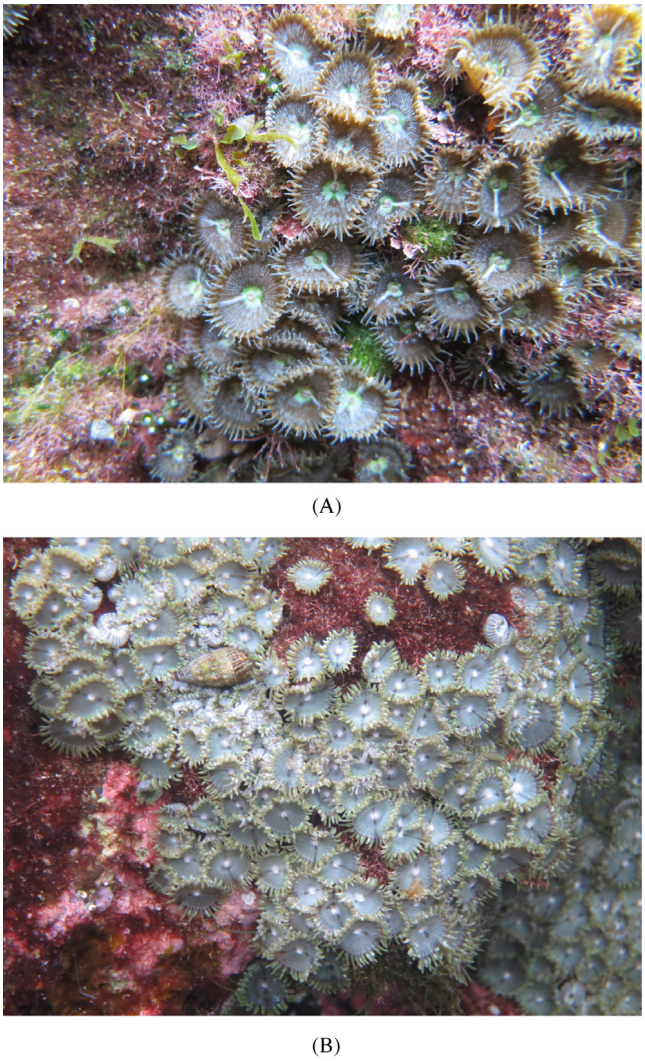
western Indian Ocean (Minchin et al., 2012), or the pantropical crab *Cronius ruber* (Lamarck, 1818) recently recorded for the first time in this region (González et al., 2017). On the other hand, native species with tropical affinities have increased in population sizes (Sangil et al., 2012). Sometimes these species are able to cause important changes in ecosystems where they settle, such as the case of the sea urchin *Diadema africanum* Rodriguez, Hernandez, Clemente & Coppard, 2013, which is a key herbivore that is capable of drastically reducing the macroalgae layer (Hernández et al., 2010). At the same time, species of temperate affinities are progressively depleting their population sizes, some known as important ecosystem-engineers, such as brown algae *Cystoseira abies-marina* (SG Gmelin) C. Agardh, 1820 (Riera et al., 2014), *Fucus guiryi* Zardi, Nicastro, E.S. Serrão & G.A. Pearson, nom. inval. (Riera et al., 2015), or the seagrass *Cymodocea nodosa* (Ucria) Ascherson (Fabbri et al., 2015).

Colonial zoanthids, sessile cnidarians of the Class Anthozoa, are one of the organisms most affected by the temperature changes (Reimer et al., 2008). Many zoanthids species that inhabit the Canary Islands have their northern or southern limit of distribution within the Archipelago, indicating their clear sensitivity to temperatures oscillations in this region. That is the case of *Palythoa* and *Zoanthus* species, which show a minimum temperature limit of tolerance for larval stages of 22 °C and 18 °C, respectively (Ryland et al., 2000). Moreover, zoanthids belonging to the suborder Brachycnemina are often zooxanthellae species. This symbiosis with dinoflagellates allows corals to better adapt to changes in temperature, due to the different types of zooxanthellas (Berkelmans and van Oppen, 2006; Rabelo et al., 2014), which has been found to be closely related to temperature (Baker et al., 2008). Additionally, their toxic chemical substances (palythoxin) against predators (Moore and Scheuer, 1971; Wiles et al., 1974) and their effective asexual reproduction (Cooke, 1976; Acosta et al., 2005) allow them to compete with other sessile species and colonize large surfaces of rocky substrate in short periods of time (Sammarco et al., 1985). Considering all these inherent biological characteristics, an expansion of these species is expected if the current trend of ocean warming continues (Reimer et al., 2008, 2016). This hypothesis is supported by recent observational data of these species in the Canary Islands. Despite previous studies on these organisms are scarce, during the last decades only a few dispersed colonies of *Palythoa canariensis* had been described in the whole Archipelago (see López Pérez, 2014; Riera et al., 2014. This contrasts with more recent surveys of intertidal and shallow subtidal habitats that have shown that their populations and those of *Zoanthus* sp. are no longer dispersed in certain sites of the Archipelago, but they can locally develop large colonies and occupy extensive areas of the substrate (mainly intertidal) once dominated by photophilic algae (Simón Otegui, 2015).

Different sessile species may provide different type of habitat complexity and heterogeneity, especially when they become dominant in the substrate and in the case of mat-forming species such as colonial zoanthids. The high survival and success rates of zoanthids in intertidal environments, could allow them to act as ecosystem engineer species (Rabelo et al., 2013) and concomitant changes in the natural ecosystem could appear, following their increasing success. For instance, several studies on the ecological effects of zoanthids have assessed their relationships with macroinvertebrates (Pérez et al., 2005; Trivedi and Vachhrajani, 2014), but there is still missing information about their effects over the smallest organisms. Marine benthic communities in intertidal rocky shores are very important from an ecological point of view and ideal for conducting scientific research (Lubchenco et al., 1991). This is due to the high diversity of different functional organisms that inhabit the intertidal zone and their ability to support important environmental gradients due to tidal oscillations. Small sedentary fauna is one of least understood and studied components of intertidal habitats. However, their ecological role is crucial, given the close relationship and influence with other trophic levels. Therefore, environmental monitoring and the study of their ecological role in tide pools ecosystems are necessary (Coull, 1988; Danovaro et al., 2007).



(A)

(B)

Fig. 1. Zoanthids species chosen in this study: (A) *Palythoa canariensis* and (B) *Zoanthus* sp.

Owing to the important ecological associations between zoanthids communities and other components of the benthic fauna (Pérez et al., 2005), as well as the observation of a recent spread of colonies of thermophilic zoanthids species at the intertidal sites of the Canary Islands, the aim of the present study was to assess the potential of two Brachycnemina species of zoanthids, *Zoanthus* sp. and *Palythoa canariesis* (Fig. 1) to modify the composition of their associated fauna, including small invertebrates, in intertidal pools of the Canary Islands in the northern coast of Tenerife Island.

2. Material and methods

2.1. Study area and in situ sampling

Two sampling sites at the northern coast of Tenerife Island were selected for each zoanthid species studied (*Palythoa canariensis* and *Zoanthus* sp.) during November–December 2015: La Barranquera

Table 1
Location and characteristics of the 16 sampled tide pools in the four study areas in northern Tenerife (pools 1–8 used for the experiment with *Palythoa canariensis* and pools 9–16 for the *Zoanthus* sp. experiment). V(L): Volume of pools in L; Zoanthids (%): percentage of coverage of corresponding zoanthid species; Algae (%): percentage of coverage macroalgae.

Pool	Site	Coordinates	Habitat	V(L)	Zoanthids (%)	Algae (%)
1	La Barranquera	28°32'18.8304″ 16°23'49.9776″	*Palythoa*	428.40	26.76 ± 8.18	63.14 ± 10.95
2	La Barranquera	28°32'18.8088″ 16°23'50.4312″	*Palythoa*	657.77	41.38 ± 14.17	49.11 ± 5.69
3	La Barranquera	28°32'16.8144″ 16°23'51.6588″	Algae	271.05	0	95.97 ± 6.64
4	La Barranquera	28°32'16.7604″ 16°23'51.2412″	Algae	265.20	0	97.67 ± 5.70
5	Punta del Hidalgo	28°34'20.0668″ 16°19'56.2044″	*Palythoa*	211.07	28.24 ± 8.3	67.79 ± 6.35
6	Punta del Hidalgo	28°34'20.5932″ 16°19'56.2044″	*Palythoa*	203.30	41.60 ± 13.94	58.67 ± 10.16
7	Punta del Hidalgo	28°34'21.2304″ 16°19'55.776″	Algae	724.88	0	107.23 ± 17.6
8	Punta del Hidalgo	28°34'21.2412″ 16°19'55.7616″	Algae	448.23	0	100.55 ± 14.19
9	Punta del Hidalgo	28°34'43.6080″ 16°19'8.6376″	*Zoanthus*	708.40	91.48 ± 6.33	19.89 ± 17.47
10	Punta del Hidalgo	28°34'43.6760″ 16°19'8.6988″	*Zoanthus*	257.92	86.78 ± 10.54	21.38 ± 1.32
11	Punta del Hidalgo	28°34'43.5000″ 16°19'9.3072″	Algae	738.36	0	107.41 ± 7.37
12	Punta del Hidalgo	28°34'43.3704″ 16°19'10.9488″	Algae	907.20	0	91.03 ± 16.96
13	Los Silos	28°23'16.3032″ 16°49'23.3364″	*Zoanthus*	979.11	85.41 ± 4.81	37.87 ± 5.75
14	Los Silos	28°23'15.8244″ 16°49'22.8432″	*Zoanthus*	651.00	87.70 ± 4.71	20.28 ± 9.48
15	Los Silos	28°23'14.6508″ 16°49'21.7190″	Algae	975.00	0	101.25 ± 3.31
16	Los Silos	28°23'14.3664″ 16°49'21.9432″	Algae	777.60	0	104.29 ± 9.78

and Punta del Hidalgo for *P. canariensis* and Los Silos and another area of Punta del Hidalgo for *Zoanthus* sp (See supplementary material). In each study zone four intertidal pools were chosen, two of them dominated by colonies of each zoanthid and two other dominated by macroalgae. A total of 16 tide pools were then selected on the fringe of the middle-lower intertidal with similar dimensions and environmental conditions (Table 1).

Coverage and composition of macroalgae and zoanthids communities of each tide pool were sampled with a photographic method, using a total of 48 quadrants of 10 × 10 cm placed randomly at the substrate. Finally, all material of three quadrants per tide pool was collected by means of scraping the surface with a spatula and keeping it in hermetic bags. A total of 48 samples of scraping material were analysed, 24 for the experiment with *P. canariensis* and 24 for the *Zoanthus* sp. experiment. Samples were fixed using formaldehyde solution 10% and transported to the laboratory.

2.2. Material examined and species identification

Photographs obtained from each quadrant deployed at experimental tide pools were analysed using ImageJ 1.45 V software. The percentage of coverage of the different species of algae, supplemented with *in situ* identifications of species, was calculated.

Samples collected from scraping quadrants were passed through a 500-μm sieve and the fraction obtained was divided in fauna and flora elements. Both were identified to the lowest possible taxonomic level. Individuals from each animal species were kept in 70% ethanol, while the flora was stored in 4% formaldehyde solution. For species identification, keys and guides available (Fauvel, 1923, 1927; Day, 1967; Cejas, 1982; Cejas et al., 1982; Cejas and Brito, 1984; Hayward and Ryland, 1990; Núñez, 1990; Afonso and Sansón, 1999; Moro et al., 2003; Sanz et al., 2003; Hernández et al., 2011; El Haddad et al., 2013; Fransen, 2014; Moro et al., 2014), as well as, WoRMS (2016) and AlgaeBase (2016) websites were used.

2.3. Data analyses

With all the data collected in the field and laboratory identification study two different experiments were designed, one to evaluate the effect of habitat modification by *P. canariensis* and another by *Zoanthus* sp., both compared with habitats dominated by macroalgae. In order to evaluate differences in the community of associated fauna at each tidal pool a multivariate analysis of variance was executed by permutations using PERMANOVA software (Anderson, 2001). A two-way design with factors "Treatment" (fixed, with two levels of variation, *P. canariensis vs.* macroalgae and *Zoanthus* sp., as appropriate) and "Site" (fixed, with two levels of variation, Punta del Hidalgo *vs.* La Barranquera and Punta del Hidalgo *vs.* Los Silos, as appropriate) was used. Abundance species data were transformed to the square root and then Bray–Curtis Bray distance was applied. Finally, a principal coordinates ordination analysis (PCO) was executed to identify the differences and similarities of the samples and to see the characterizing species associated with each studied habitat.

In order to characterize the communities in intertidal pools, species richness (total number of species) and Shannon diversity indexes were calculated, from the multivariate matrix of species abundances in each experiment. These diversity indexes were analysed using univariate ANOVAs executed by permutations (Anderson, 2001). Two-way models with the same previous design and Euclidean distances of the raw data were used.

In analyses of variance, whenever enough permutations were not obtained for a valid test, the *p*-values were corrected with the Monte Carlo method (Anderson and Robinson, 2003). Also, the

Table 2
(A) Results of PERMANOVA analysis of communities of small invertebrates associated with two different habitats, one dominated by *Palythoa canariensis* and other by macroalgae, in two intertidal sites of Tenerife Island (La Barranquera and Punta del Hidalgo). Pair-wise tests analyses examining the significant interaction of factors "Treatment × Site", showing differences in communities between (B) the two levels of factor "Treatment" *(Palythoa canariensis vs.* macroalgae) at each study site and (C) the two levels of the factor "Site" (Punta del Hidalgo *vs.* La Barranquera) at both kind of habitats studied.

(A) Source of variation	df	SS	MS	Pseudo-F	*p* (MC)
Treatment	1	9597.6	9597.6	8.58	0.001
Site	1	12 834	12 834	11.48	0.001
Tr × S	1	4095.8	4095.8	3.67	0.003
Residual	20	22 369	1118.4		
Total	2323	48 896			
(B)	*t*	*p* (MC)	(C)	*t*	*p* (MC)
La Barranquera	2.45	0.001	*P. canariensis*	2.79	0.002
Punta Hidalgo	2.48	0.001	Macroalgae	2.71	0.003

significant terms of the models were *a posteriori* analysed by pair-wise tests executed by permutations (Anderson, 2001).

The PRIMER 6 & PERMANOVA + v.1.0.1. package was used to conduct all statistical procedures.

3. Results

In tide pools dominated by macroalgae communities, algae stands represented over 92% of coverage of the substrate, while colonies of the zoanthids did not occur (Table 1). Regarding zoanthids dominated habitats, studied tide-pools showed percentages cover of *P. canariensis* ranging from 19.54 to 57.63% and from 79.59 to 98.13% cover in the case of *Zoanthus* sp. colonies (Table 1). At the same time, coverages of algae stands were reduced in these habitats, representing 48.62 to 81.42% of substrate cover in the case of pools with *P. canariensis* and 42.76 to 12.33% in habitats dominated by *Zoanthus.*

A total of 10,607 specimens belonging to 102 different species were identified from the fauna on scrapings of intertidal pools. The most diverse taxonomic group was annelids with 44 different species, followed by molluscs and arthropods with 31 and 18 identified species respectively. Regarding macroalgae communities of intertidal pools, a total of 32 different species were identified: 6 species from Phylum Chlorophyta, 13 Rhodophyta y other 13 species from Ochrophyta (see supplementary material).

3.1. *Palythoa canariensis* effects on associated communities of small invertebrates

PERMANOVA analysis of the fauna associated with tidal pools dominated by *P. canariensis* showed a significant interaction of the factors "Treatment × Site" (Table 2A). The abundance and species composition of the fauna varied between habitats dominated by *P. canariensis* and those dominated by macroalgae, in different ways depending on the site studied. *A posteriori* pair-wise comparisons found differences in the communities associated with *P. canariensis* and those associated to macroalgae habitats in the two sites studied (Table 2B). Similarly, significant differences between study sites were shown both for communities associated to *P. canariensis* and macroalgae (Table 2C). These results are clearly visualized in the PCO analysis, which accounted for ≈54% of the total variability of the data recorded (Fig. 2). The ordination of samples in the graph showed clear differences in the composition of communities studied, both for sampling conducted in tide pools dominated

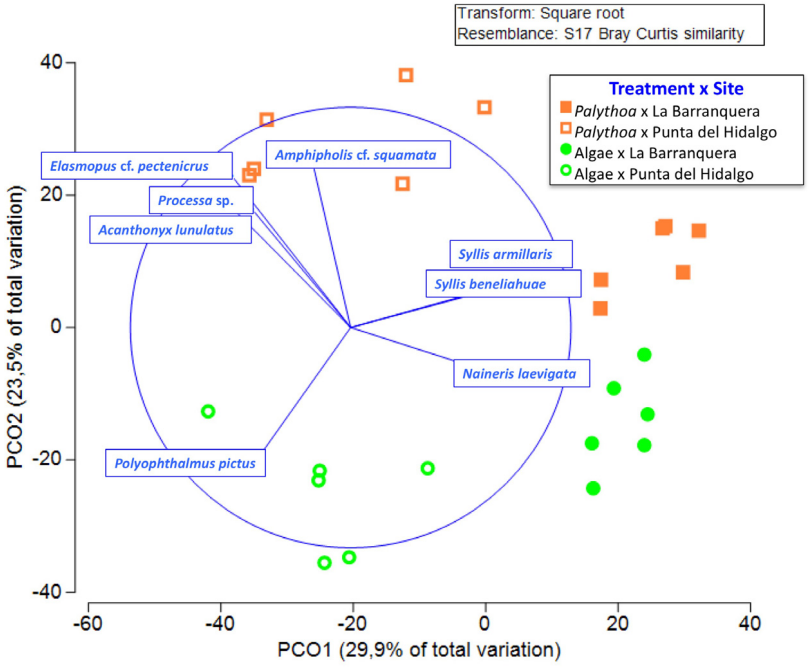


Fig. 2. Principal Coordinates (PCO) graph showing the differences in the abundance and composition of the associated fauna with tide pools dominated by *Palythoa canariensis* and those dominated by macroalgae in two sites in northern Tenerife (La Barranquera and Punta del Hidalgo).

by zoanthids colonies and by algae communities. Furthermore, a greater difference between the studied communities in areas of *P. canariensis* and algae in Punta del Hidalgo than in La Barranquera was shown, evidenced by greater segregation between points belonging to each habitat at the former site (Fig. 2). Species that best explain the variability found in the data are represented as vectors in the PCO (Fig. 2). Within the associated fauna that dominated and characterized *P. canariensis* habitats we found arthropods that were more abundant in Punta del Hidalgo, such as *Elasmopus* cf. *pectenicrus* (Order Amphipoda), *Processa* sp. and *Acanthonyx lunulatus* (Order Decapoda), as well as the echinoderm *Amphipholis* cf. *squamata* (Class Ophiuroidea). The annelids *Syllis armillaris* and *S. beneliahuae* (Family Syllidae) were especially abundant in habitats dominated by *P. canariensis* in La Barranquera. *Polyophthalmus pictus* (Family Ophelidae, Annelida) and *Naineris laevigata* (Family Orbinidae, Annelida) were the species that characterized to a greater extent the habitats dominated by macroalgae at Punta del Hidalgo and La Barranquera respectively (Fig. 2).

Analysis of the variance of diversity indexes showed that the total number of species of the studied communities varied significantly between levels of the factors "Treatment" and "Site" (Table 3A). Communities associated to *Palythoa canariensis* had a higher richness of species (36.67 ± 6.36 species) than those associated with macroalgae (30 ± 6.45 species), and total numbers of species of invertebrates were higher in La Barranquera (37.75 ± 5.41 species) than in Punta del Hidalgo (28.92 ± 5.87 species). A significant interaction of the factors "Treatment × Site" was found when analysing results of the Shannon diversity index (Table 3B), so that species diversity varied depending on the site and habitats considered. *A posteriori* pair-wise analyses showed significant differences between the diversity index recorded in habitats dominated by *P. canariensis* and in those dominated by macroalgae only in the site of Punta del Hidalgo ($t = 3.35$; p-value $= 0.0014$), where communities associated to *P. canariensis* showed a higher Shannon diversity index (2.33 ± 0.46) than communities within macroalgae habitats (2.17 ± 0.19). Similarly, significant differences between the site of Punta del Hidalgo and La Barranquera were detected only in sampling conducted in pools dominated by *P. canariensis* ($t = 2.35$; p-value $= 0.037$), showing Punta del Hidalgo more diverse communities in tide pools dominated by *P. canariensis* (2.38 ± 0.3) than La Barranquera (2.12 ± 0.37).

3.2. *Zoanthus* sp. effects on associated communities of small invertebrates

The multivariate analysis of the fauna associated with tidal pools dominated by *Zoanthus* sp. colonies showed a significant interaction of factors "Treatment × Site" (Table 4A). The abundance and species composition of the fauna studied varied between habitats dominated by the zoanthid and those dominated by macroalgae, differently according to the site studied. *A posteriori* pair-wise comparisons found differences between the abundance and composition of invertebrates associated with *Zoanthus* sp. and those associated with macroalgae habitats in the two sites studied (Table 4B), although they were more evident in Punta del Hidalgo than in Los Silos (Fig. 3). On the other hand, site-specific significant differences were only detected in communities in tide pools dominated by macroalgae, while the fauna community associated with *Zoanthus* sp. did not differ significantly between sites (Table 4B). These results are shown in the PCO analysis, which explained approximately 44.2% of the total variability of data recorded (Fig. 3). The ordination of samples in the graph showed clear differences between sampling sites in the composition of communities associated with macroalgae habitats, while sampling points corresponding to pools dominated by *Zoanthus* sp. at both study sites overlapped and showed no clear segregation (Fig. 3). Regarding the species that best explained the variability found in the data, the species that dominated and characterized *Zoanthus* sp. habitats, regardless the site considered, were the annelids *Linopherus canariensis* (Family Amphinomidae) and *Syllis armillaris* (Family Syllidae), the mollusc *Cardita calyculata* (Class Clamshell) and the sipunculid *Phascolosoma (Phascolosoma) stephensoni* (Fig. 3). Within the associated fauna that dominated and characterized macroalgal habitats we found *Tanais* cf. *dulongii* (Order Tanaidacea, Arthropoda), as well as the mollusc *Barleeia unifasciata* specifically in Punta del Hidalgo and the annelid *Amphiglena mediterranean* (Family Sabellidae) in Los Silos (Fig. 3).

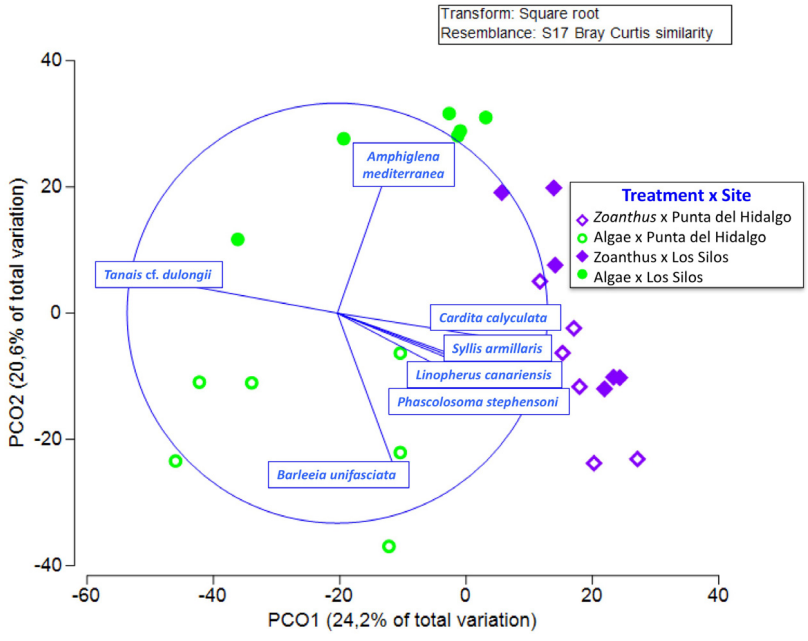


Fig. 3. Principal Coordinates (PCO) graph showing the differences in the abundance and composition of the fauna associated with tide pools dominated by the zoanthids *Zoanthus* sp. and those dominated by macroalgae in two site in northern Tenerife (Punta del Hidalgo and Los Silos).

Table 3
Results of permutational ANOVA analyses of (A) species richness (number of species) and (B) Shannon diversity index of communities of small invertebrates associated with two different habitats (Treatments), one dominated by *Palythoa canariensis* and other by macroalgae, in two intertidal sites of Tenerife Island (La Barranquera and Punta del Hidalgo).

		(A) Specific richness				(B) Shannon Index			
Source of variation	df	SS	MS	Pseudo-F	*p* (MC)	SS	MS	Pseudo-F	*p* (MC)
Treatment	1	266.67	266.67	12.28	0.002	0.15	0.15	1.52	0.227
Site	1	468.17	468.17	21.56	0.001	0.43	0.43	4.54	0.044
Tr × S	1	0.17	0.17	7.68E−3	0.924	0.40	0.40	4.18	0.056
Residual	20	434.33	21.72			1.90	9.49E−2		
Total	23	1169.3				2.87			

Table 4
(A) Results of PERMANOVA analysis of communities of small invertebrates associated with two different habitats, one dominated by *Zoanthus* sp. and other by macroalgae in two intertidal sites of Tenerife (Punta del Hidalgo and Los Silos). Pair-wise tests analyses examining the significant interaction of two factors "Treatment × Site", showing differences in communities between (B) the two levels of factor "Treatment" (*Zoanthus* sp. *vs.* macroalgae) at each study site and (C) the two levels of factor "Site" (Punta del Hidalgo *vs.* Los Silos) at both kind of habitats studied.

(A) Source of variation	df	SS	MS	Pseudo-F	*p* (MC)
Treatment	1	8459.7	8459.7	5.84	0.001
Site	1	6360.1	6360.1	4.39	0.004
Tr × S	1	2920.1	2920.1	2.01	0.045
Residual	20	28 990	1449.5		
Total	232.3	46 730			
(B)	*t*	*p* (MC)	(C)	*t*	*p* (MC)
Punta del Hidalgo	2.07	0.001	*Zoanthus* sp.	1.21	0.211
Los Silos	1.87	0.009	Macroalgae	2.20	0.003

Table 5
Results of permutational ANOVA analyses of (A) species richness (number of species) and (B) Shannon diversity index of communities of small invertebrates associated with two different habitats (Treatments), one dominated by *Zoanthus* sp. and other by macroalgae, in two intertidal sites of Tenerife Island (Punta del Hidalgo and Los Silos).

		(A) Specific richness				(B) Shannon index			
Source of variation	df	SS	MS	Pseudo-F	*p* (MC)	SS	MS	Pseudo-F	*p* (MC)
Treatment	1	266.67	266.67	12.28	0.001	1.72	1.72	23.69	0.001
Site	1	468.17	468.17	21.56	0.001	0.14	0.14	1.94	0.179
Tr × S	1	0.17	0.17	7.68E−3	0.862	0.18	0.18	2.47	0.130
Residual	20	434.33	21.72			1.44	7.24E−2		
Total	23	1169.3				3.48			

Analysis of variance of diversity indexes results, including the total number of species (species richness) and the Shannon diversity index, revealed the existence of significant differences at the level of the factor "Treatment" for both studied variables (Table 5A & B). Communities associated to *Zoanthus* sp. habitats showed higher values for these indexes (species richness: 27.08 ± 6.14 species; Shannon diversity: 2.45 ± 0.23), in comparison with macroalgae habitats (species richness: 20.67 ± 6.67 species; Shannon diversity: 1.91 ± 0.33). Also site-specific differences were detected only when analysing species richness (Table 5A), occurring higher numbers of species in Los Silos (26.42 ± 6.9 species) than in Punta del Hidalgo (21.33 ± 6.55 species).

4. Discussion

The present study evidenced the capacity of the zoanthids *P. canariensis* and *Zoanthus* sp. to modify the intertidal pools ecosystems of the Canary Islands. The thermophilic affinities of these species in the current context of rising ocean temperatures (Kumari et al., 2016), in addition to their asexual reproduction abilities and competing ability (Poriya and Kundu, 2017), have allowed them to colonize large areas of the littoral rocky substrate, acting as ecosystem engineer species. Results of present study showed that these zoanthids species have the ability to increase the complexity of the ecosystems and change the composition of local biodiversity. Their presence in substrate covers above ≈25% (Table 1) significantly increased species richness and diversity of the biota. Additionally, such relatively high coverages of zoanthids colonies in the intertidal habitat is in sharp contrast with the dispersed pattern of the distribution of the colonies in the Canarian Archipelago previously recorded in the literature, especially in the case of *Palythoa canariensis* (Riera et al., 2014).

The hereby study found a substantial modification of the associated fauna, as well as an increase in species diversity and richness in habitats dominated by colonies of both zoanthids. The abundance and composition of the invertebrate fauna associated to intertidal pools dominated by *Zoanthus* (≈85%–92% cover, Table 1) were more homogeneous, regardless the site studied, than that associated to *P. canariensis* colonies (≈26%–42% cover, Table 1). Therefore, it is demonstrated that especially *Zoanthus* sp. can be recognized for its transformative effect in the intertidal habitat, being able to produce a homogenization of the communities of different sites in terms of the abundance and composition of associated invertebrate fauna. The reason for these results seems to be the greater capacity of *Zoanthus* to cover almost completely the substrate, not only on illuminated substrates but also in cryptic environments such as crevices and hollows. Similar results have been observed in other previous studies, in which this kind of colonial species were considered good competitors within the group of cnidarians (Sebens, 1982; Karlson, 1983; Poriya and Kundu, 2017).

Previous research has found associations between certain invertebrate species and different zoanthids, such as *Palythoa mutuki* (Trivedi and Vachhrajani, 2014; Chakravarty et al., 2016), *Palythoa caribaeorum* (Pérez et al., 2005), or *Zoanthus sansibaricus* (Chakravarty et al., 2016). In all cases the most abundant group of associated species were mollusks and arthropods. This study also showed highest abundances of mollusks within habitats dominated by zoanthids, but polychaeta were abundant as well (Figs. 2

and 3). These differences are probably due to the fact that the mesofauna associated was studied instead of just the macroinvertebrates. The contrasting composition and relative abundances of communities of small invertebrates associated with *P. canariensis* and *Zoanthus* sp. in comparison to macroalgae dominated habitats, demonstrated the capacity of these mat-forming colonial organisms to transform the community. For instance, an increase of certain mollusk species within the colonies that cover the substrate was detected, as in the case of other coral species (Martinez et al., 2012).

Analyses examining species composition of the studied intertidal habitats found certain characterizing species for environments dominated by colonies of both zoanthids species. Some of them can be considered as potential new guests and even predators of these zoanthids in the Canary Islands. For instance, it is known that polychaete of the family Syllidae, such as the species *Syllis armillaris* commonly found associated with both zoanthids colonies, are able to colonize various types of substrates, being especially abundant between layers of living and dead corals (Fauchald and Jumars, 1979). Some authors claim that their carnivorous diet could be based on hydroids, bryozoans and other colonial invertebrates (Fauchald and Jumars, 1979; Giangrande et al., 2000), and others have demonstrated their abilities to dominate on altered benthic habitats (Çinar, 2003). Hence, pools dominated by zoanthids in the Canary Islands could provide a suitable refuge and food source environment for these species. A similar result was found in Brazil where species of the same family were associated with *P. caribaeorum* (Pérez et al., 2005). Another errant polychaete that frequently occurred associated with *Zoanthus* sp. was *Linopherus canariensis.* This annelid species belongs to the family Amphinomidae, which includes a group of species known to be commonly associated with cnidarians (Ebbs, 1966; Barroso and Paiva, 2007). However, the species most studied in this family is *Hermodice carunculata* (Pallas, 1766), which is known to actively feed on several coral species, anemones and zoanthids, specifically species of the genus *Zoanthus* (Sebens, 1982; Francini-Filho and Moura, 2010; De Assis et al., 2017). Therefore, a possible association between the presence of *L. canariensis* and colonies of *Zoanthus* sp., probably favoured by the biology and feeding habits of the polychaete is suggested.

In the case of tide pools dominated by colonies of *P. canariensis*, the presence of the echinoderm *Amphipholis* cf. squamata was especially relevant. This kind of omnivorous species has been previously recorded to be prevalent in bryozoans and many other types of intertidal substrates, besides being also abundant among algae stands (Jones and Smaldon, 1989; Boissin et al., 2016). Similarly, other Ophiuroidea were found associated with *P. mutuki* by Trivedi and Vachhrajani (2014) and Chakravarty et al. (2016).

All the changes recorded in the studied intertidal communities by means of current experimental procedures, showed the high adaptability of small invertebrates to the presence of colonies of zoanthids in the ecosystem. Therefore, several species may be able to take advantage of the recent population increase of these colonial anthozoans in the Canary Islands. Given the projected increases in SST within the current climate change scenario that will keep favouring the expansion of thermophilic zoanthids species *Palythoa canariensis* and *Zoanthus* sp., important changes in the biodiversity of the intertidal zones are expected, especially in subtropical regions such as the Canary Islands. Despite it would be desirable to go deeper into the ecological relationships between specific mesoinvertebrate species and the zoanthids, changes in the abundance, composition and diversity of species associated with these key colonial organisms could create potential alterations and in extreme cases a disequilibrium in the natural ecosystem, due to the new contribution of habitable substrate. This should be taken into account for future ecology and biology research of these species and for the planning of adaptation and mitigation measures against climate change processes.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2018.03.006.

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